ACOUSTICAL COMMUNICATION IN *CHRYSOPA RUFILABRIS* (NEUROPTERA: CHRYSOPIDAE), A GREEN LACEWING WITH TWO DISTINCT CALLS

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Abstract.—Like its close relative *Chrysopa carnea* Stephens, *C. rufilabris* Burmeister produces substrate-borne low frequency sound by vibrating the abdomen vigorously in mid-air. These vibrations are necessary components of normal courtship and mating in the species. Males produce short (⅓ sec) calls early in courtship or when alone, but shift to much longer (4–7 sec) calls as courtship progresses. Both types of calls consist of single volleys of abdominal vibration and are characterized by a fairly constant frequency of 14 to 18 strokes/second; the long call shows distinctive amplitude modulation. Females respond to male calls of either type only with short calls, similar to those of males but of different amplitude structure. The male's short call elicits single replies from the female while his long call stimulates multiple replies at 1.5–3.0 second intervals. Gross differences between the calls of *C. rufilabris* and *C. carnea* suggest that acoustical communication helps to isolate sympatric lacewing species reproductively from one another.

It has been shown recently that green lacewings of the genus *Chrysopa* (broad sense) initiate and maintain courtship by exchanging volleys of abdominal vibration or jerking (Henry, 1979). Such volleys are typically produced in fairly long sequences ("calls") of species-characteristic structure by members of both sexes. Actual drumming of the abdomen on the substrate does not occur; instead, the low-frequency oscillations are transmitted to any light-weight, compliant substrate through the legs of the calling insect and thence to appropriate sense organs on the legs of other nearby lacewings (unpublished data). There is no evidence to support the appealing hypothesis proposed by Riek (1967), elaborated by Henry (1979), and accepted by Eichele and Villiger (1974) that abdominal jerking produces high-frequency air-borne sounds by stridulation.

Although "calling" behavior has been described in detail only for *Chrysopa carnea* Stephens (Henry, 1979), preliminary observations (Henry, 1979

and unpublished data) indicate that complex, highly individual patterns of jerking exist in several other lacewing species sympatric with *C. carnea* in eastern North America. These patterns are particularly elaborate and distinctive in the closest relatives of *C. carnea* like *C. downesi* Banks (manuscript submitted for publication), *C. harrisii* Fitch, and *C. rufilabris* Burmeister, but can also be identified in more distantly related forms like *C. oculata* Say, *C. nigricornis* Burmeister, *C. chi* Fitch, and *C. quadripunctata* Burmeister. The species-specific nature of calling pattern variation suggests that abdominal jerking is or has been important to the reproductive isolation of these lacewing species.

Here, I describe in detail the characteristic acoustical patterns of *Chrysopa rufilabris*, a species showing broad geographical and temporal coincidence with and morphological similarity to *C. carnea* (Bram and Bickley, 1963). This common lacewing differs greatly from *C. carnea* not only in the structure of its calls but also in its capacity to produce two distinctive types of calls in different situations. In addition, marked sexual dimorphism of the acoustical signal characterizes prolonged duets between partners in *C. rufilabris* but not in *C. carnea*. The evolutionary and phylogenetic significance of these findings is then discussed briefly.

Methods and Materials

I collected adults of *C. rufilabris* at the edges of old fields from July to October during 1977 and 1978 and placed them in breeding colonies supplied with water and Wheast™ diet (Hagen and Tassan, 1970). This and other species were identified using the keys of Bram and Bickley (1963). Eggs were removed daily and larvae reared on ether-killed *Drosophila* spp., as described in an earlier paper (Henry, 1979). Collecting sites included Storrs, Connecticut; Woods Hole, Massachusetts; and Rensselaerville, New York. Separate populations were maintained only until calling patterns were shown to be identical in lacewings from all three areas. First through third laboratory generations were tested for reproductive and acoustical behavior.

I recorded and photographed jerking activity using the techniques and equipment of the earlier study (Henry, 1979). A crystal phonograph cartridge picked up substrate vibrations produced in a thin plastic membrane by calling lacewings and fed these signals to a storage oscilloscope. Experiments were conducted and observations recorded primarily under low-intensity red light during the insects' "night." The results and conclusions that follow are based upon approximately 133 hours of observation of lacewing behavior on 77 days over a two-year period, representing the detailed sexual activities of 14 males and 10 females. Of these, 12 males and 9 females, in 14 different pairwise combinations, participated in 171 heterosexual calling duets. I also tabulated data on 10 homosexual duets involving six males in three separate pairings. Six copulations (6 different couples and 12

different individuals) and 16 near-copulations (6 different couples; 5 different males, 4 females) occurred during the course of the study. Reference to "significant differences" indicates that the means of two samples were demonstrated to differ from one another by a 2-tailed t-test using confidence limits of 95 percent or better.

RESULTS

As in *C. carnea*, mating in *C. rufilabris* is preceded by a long, well-defined courtship in which the partners exchange volleys of abdominal vibration. The same stages of search, antennal contact, mouthpart contact, abdominal approach, abdominal contact, and copulation characterize mating behavior in both species, and copulatory positions and duration are also similar. However, during abdominal approach, individuals of *C. rufilabris* do not raise and flutter their wings; instead, a short period of "wingbumping" ensues, during which both sexes repeatedly and synchronously bring their paralleled bodies together with some force at ½ to ¾ sec intervals so that adjacent wing surfaces of the two insects slap one another. After 5 to 15 bumps, abdominal contact is established when the partners suddenly and simultaneously raise their wings; copulation quickly follows.

Sexually receptive males without partners periodically produce short bursts of abdominal jerking, hereafter termed "short calls." These calls last about ⅓ sec and consist of 5 or 6 vertical strokes or jerks of the abdomen produced at a frequency of 15 to 18 strokes (cycles) per second (Fig. 1A, B; Table 1). The insect will repeat his short call sporadically every 5 to 30 seconds, but no predictable between-call interval appears to characterize this behavior pattern. Extreme magnification of each stroke of a typical volley (Fig. 1C) reveals no significant sub-structure that could indicate the presence of higher orders of abdominal vibration: the high-frequency oscillations ($\sim$500 cps) seen in the photograph derive from the resonant properties of the substrate and are induced whenever the membrane is struck.

If conditions are right, the short call of such a male may trigger production of a similar but often weaker call from a nearby (less than 15 cm) female. Thus, a duet between the partners will be established: the female promptly replies to each male volley within ½ to 2 seconds of the latter's inception (Fig. 1B, D; Table 2). Typically, such exchanges are repeated every 6 or 7 seconds, although this repetition interval is not at all constant. On the average, the female's short call is slightly but significantly longer ($\bar{x} = 0.42$ sec) and lower in frequency (14 to 17 strokes/sec) than that of the male; in fact, these differences were maintained in 8 out of 10 and 7 out of 8 duets, respectively.

Short-call duets are usually quite ephemeral, since the male soon initiates much longer volleys of abdominal jerking. Each "long call" (Fig. 1E; Table 1) begins like a short call with a burst of jerking lasting about ⅓ sec; how-
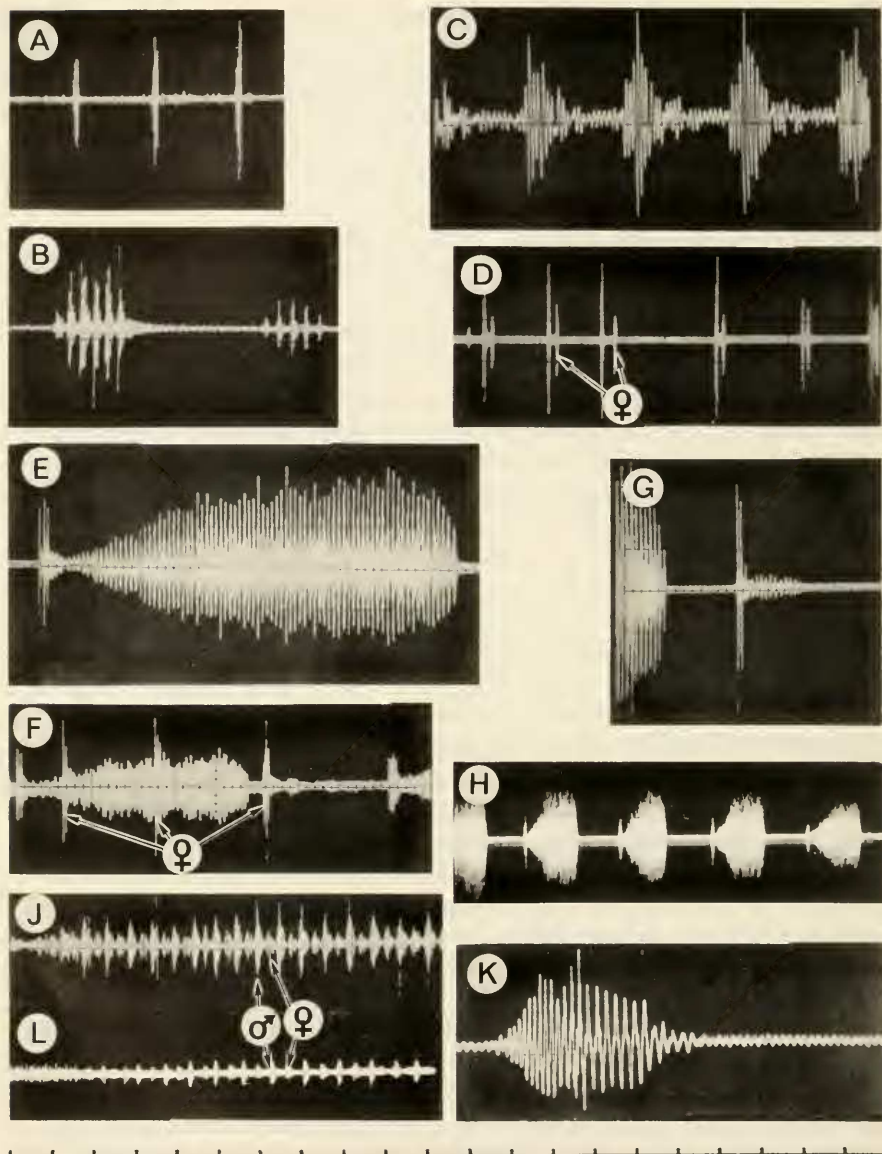
Fig. 1. Oscillographs of abdominal jerking behavior in males and females of *Chrysopa rufilabris* (A–H), *C. carnea* (J and K), and *C. chi* (L), recorded at different sweep speeds (see scale). A = three short calls by male; 2.00 sec/div. B = detail of male-female duet, short-call type; 0.20 sec/div. C = enlargement of a portion of male short call, showing abdominal strokes (major spikes) and substrate resonance (fine oscillations); 0.02 sec/div. D = prolonged male-female duet, short-call type; 5.00 sec/div. E = male long call; 0.50 sec/div. F = male-female duet, long-call type; 1.00 sec/div. G = detail of a female call delivered after conclusion of

ever, rather than ceasing altogether, abdominal motions persist at low intensity for several cycles and then increase to progressively higher amplitudes over a 4 to 7 second period. This pattern is quite stereotyped, varying only in overall duration. In frequency characteristics, the long call is slightly but significantly different from the short call, averaging 18.20 ± 1.11 strokes/sec (N = 116) versus 16.58 ± 1.68 strokes/sec (N = 79); internal frequency differences between the initial short volley and later portion of the long call are inconsequential.

The female's response to the male's long call closely resembles that to his short call, except that it is repeated every 1.5 to 3.0 seconds while the male's call is in progress (Fig. 1F; Tables 1 and 2). Often but not always, one final female volley is produced a second or two after the male stops jerking (Fig. 1G); when this occurs, it can be seen that each female call may actually persist one or two seconds and is characterized by two or three intense abdominal strokes followed without a break by 15 to 30 strokes of much lower intensity. Thus what appear to be short responses to the male's long call may instead be longer calls whose low-intensity portions have been masked by the male signal. Nonetheless, it is clear that this female call is quite distinct in length and amplitude characteristics from male calls of both the short and long variety.

When a serious male-female duet of the long-call type has been established, jerking episodes of the sort just described are repeated regularly every 7 to 18 seconds ($\bar{x} = 9.72 \pm 4.81$, N = 75; Fig. 1H and Table 2). As the threshold for mating is approached, wing-bumping and abdominal jerking occur simultaneously, with a tendency for male calling to become continuous for many seconds. Copulation is of relatively short duration, averaging 6 minutes (N = 5).

Homosexual duets are not structurally distinct from the heterosexual ones described above (Tables 1 and 2). Usually, two males exchanged short calls; however, on one occasion, I observed a male assuming the female role in responding to the long call from its partner.

Discussion

The results of the present study greatly extend and clarify those obtained from preliminary work published earlier (Henry, 1979). Several minor misconceptions concerning male-female duets and the precise form and fre-

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male's long call in a duet; 0.50 sec/div. H = prolonged male-female duet, long-call type, with female signal masked by male's; 5.00 sec/div. J = male-female duet, *C. carnea*; 2.00 sec/div. K = detail of one volley of abdominal jerking produced by male of *C. carnea*; note frequency modulation; 0.10 sec/div. L = male-female duet, *C. chi*; note similarity to J; 2.00 sec/div.

Table 1. Comparison of important characteristics of long and short calls of both sexes of *Chrysopa rufilabris* in four different situations. Duration and repetition intervals are in seconds, frequency in abdominal strokes/second; standard deviations are included. Sample sizes are entered in parentheses: The larger figure represents the total number of calls measured, the smaller figure the number of individuals that produced three or more of such calls. Figures may not tally with those given in text due to pooling or splitting of samples.

	Short Calls				Long Calls			
	Duration	Frequency	No. of Abd. Strokes	Repetition Interval	Duration	Frequency	No. of Abd. Strokes	Repetition Interval
Male Heterosexual Calls (All)	0.33 ± 0.07 (10/78)	16.58 ± 1.68 (10/79)	5.62 ± 1.05 (9/86)	5.61 ± 3.69 (9/117)	5.15 ± 1.23 (12/183)	18.20 ± 1.11 (10/116)	50–120 (10/12)	10.60 ± 4.79 (11/136)
Male Homosexual Calls (All)	0.37 ± 0.07 (3/4)	16.19 ± 0.63 (3/4)	5.75 ± 0.96 (3/4)	10.53 ± 10.19 (3/10)	3.60 (1)	17.37 (1)	63 (1)	5.25 (1)
Female "Answers" to Short Calls	0.33 ± 0.05 (4/33)	15.27 ± 0.89 (4/35)	5.36 ± 0.86 (4/33)	—	—	—	—	—
Female "Answers" to Long Calls	0.57 ± 0.33 (2/21)	16.74 ± 1.14 (2/20)	10.47 ± 6.95 (2/19)	2.47 ± 0.96 (6/70)	—	—	—	—

Table 2. Time (in seconds) elapsing between volleys of abdominal jerking produced by individuals of *Chrysopa rufilabris* in heterosexual and homosexual duets. Standard deviations and sample sizes as in Table 1, except for the smaller number in parentheses which represents the number of different couples that called to each other three or more times.

	Short Calls			Long Calls		
	Male-Male Interval	Male-Female (or Male$_1$- Male$_2$) Interval	Female- Female Interval	Male-Male Interval	Male-Female (or Male$_1$- Male$_2$) Interval	Female- Female Interval
Male-Female Duets	6.25 ± 3.93 (5/60)	1.07 ± 0.71 (5/68)	4.69 ± 3.59 (–/4)	9.72 ± 4.81 (8/75)	1.85 ± 0.71 (9/76)	2.47 ± 0.96 (6/70)
Male-Male Duets	3.88 ± 0.98 (2/6)	5.73 ± 4.77 (6/17)	—	5.25 (1)	—	—

quency of the male's long call are corrected here, illustrating the problems that can arise when highly variable behavior is studied in too few individuals.

The most striking aspects of abdominal jerking behavior in *C. rufilabris* include its sexual dimorphism, its duality of expression in individual males, and its organization into long continuous volleys rather than extended sequences of short volleys. *Chrysopa carnea*, by contrast, produces but one type of short volley in both sexes and under all conditions, repeating the same phrase regularly every second or so when calling (Henry, 1979). Both species establish calling duets during courtship and mating, but the precise, non-overlapping alternation of male and female volleys in *C. carnea* (Fig. 1J) has no counterpart in the sexually dimorphic, superimposed exchanges of *C. rufilabris*. Another difference concerns the frequency of abdominal vibration, which is very low and relatively constant in any given long or short volley of *C. rufilabris* but higher and modulated from 100 strokes/sec to 35 strokes/sec in each volley of *C. carnea* (Fig. 1K). Acoustical data on the other lacewing species listed earlier in this paper are incomplete, but suggest that calls in *Chrysopa* are generally organized into sequences made up of discrete, repeating volleys of jerking as in *C. carnea* rather than consisting of long, isolated phrases like those of *C. rufilabris*. Sexual dimorphism of calling pattern is also unique in *C. rufilabris* among lacewings tested, but evidence exists confirming two distinct calls in both sexes of *C. nigricornis* (unpublished data).

Traditional speciation hypotheses (Mayr, 1963; Brown and Wilson, 1956) predict greatest divergence in calls between (among) the most closely related species of lacewings, assuming that such acoustical communication is important to the reproductive isolation of species. *Chrysopa carnea* and *C. rufilabris* are closely related members of the subgenus *Chrysoperla* Steinmann (=genus *Chrysoperla* according to Semeria, 1977): their radically dif-

ferent calls offer circumstantial confirmation of the above prediction, especially since representatives of the distinct subgenus *Chrysopa s. str.* produce calls more similar to those of *C. carnea* than to those of *C. rufilabris* (e.g., see Fig. 1L for a heterosexual duet in *C. chi* that is remarkably convergent on that of *C. carnea*). It seems likely, therefore, that acoustical signals produced by abdominal jerking function as reproductive isolating mechanisms in sympatric lacewings, particularly in those of the structurally homogeneous subgenus *Chrysoperla*.

Acknowledgments

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